# Effects of multiple herbivore guilds on population dynamics are subadditive in a model forb species

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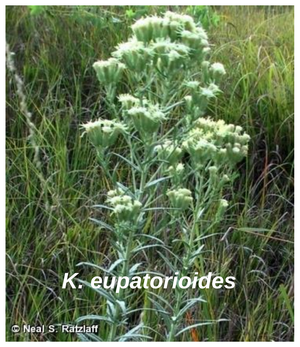
## Introduction

- We have a good understanding of how individual herbivore guilds affect herbaceous communities
  - Invertebrate herbivores reduce grassland biomass and change species composition dramatically [1]
  - Bison reduce grass biomass and increase forb cover [2]
  - Small mammals have weak effects [3]
- Few studies quantify how multiple co-occurring herbivore guilds jointly impact populations and communities
  - Potential for super- or subadditive effects
  - Many ecosystems house multiple herbivores
  - Critical to predicting impacts of herbivore declines, extirpations, or reintroductions
- Here, we use *Kuhnia eupatorioides* at Konza LTER to ask whether effects of herbivores tend to be additive, super-, or subadditive
  - We measure individual vital rates (survival, growth, recruitment) to dissect mechanisms driving sub- or super-additivity




## Results

- λ is lowest when all three herbivore guilds are present
- Bison reduce λ and survival, insects and small mammal effects are variable (Fig 1A, B)
- Bison increase growth, insect and small mammal effects are variable (Fig 1C)
- Insects strongly increase fruits per biomass; bison and small mammals weakly increase fruits per biomass (Fig 1D)
- After controlling for initial plant size & block, herbivore exclosure treatment is present in the best-fit model only for growth (Fig 1C)
- No recruitment occurred

**Predicted vs. observed responses to multiple herbivore guilds**

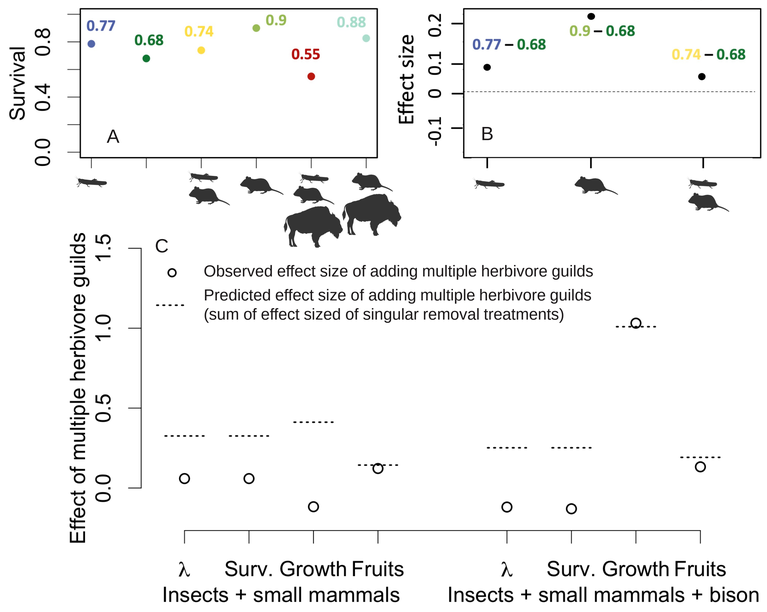



**Fig. 3.** Additive effects of multiple herbivore guilds vs. observed effects of multiple herbivore guilds. A and B show an example of how the points in C (for survival in the presence of insects + small mammals) are calculated. Namely, A shows herbivore exclosure treatment effects on survival (as in Fig. 2B), B shows the relative effect size of adding singular and multiple herbivore guilds. C shows the observed (points) and predicted (lines, based on effects of each herbivore guild alone) effects of multiple herbivore guilds on population dynamics.

**Population-level responses to three herbivore guilds**

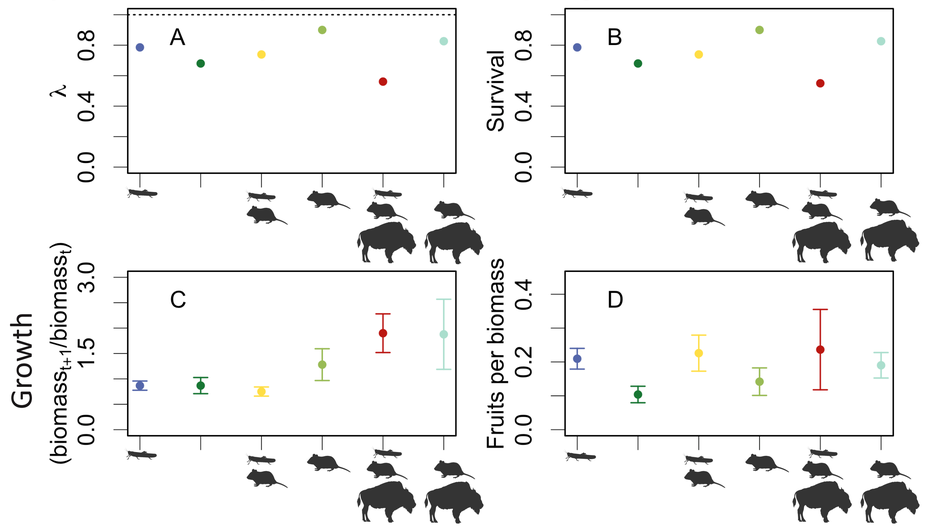



**Fig. 2.** Herbivore exclosure treatment effects on λ (A), survival (B), growth (C), and fruits per biomass (D). Bars indicate standard errors. There are no SE for survival or λ, because these are calculated from counts across all blocks. Recruitment (into occupied plots) was zero for all herbivore exclosure treatments, so we do not show this response.

- Effects of multiple herbivore guilds on λ are always subadditive
  - Weaker effects of 2 (or 3) herbivores together than their singular effect sizes would predict
- Survival and growth generate subadditivity for insects + small mammals
  - Positive impacts of both insects and small mammals arise from reduction in grass biomass & lower competition?
  - Reduction in competition can only increase survival & growth to a point– plants are limited by abiotic stress?
- Only survival generates subadditivity for insects + small mammals + bison
  - Effects of insects are minimal for growth, resulting in additivity of insects and small mammals + bison herbivore exclosure treatment
  - Effects of insects are positive for survival, resulting in subadditivity

## Methods

**ConSME experimental plot design**

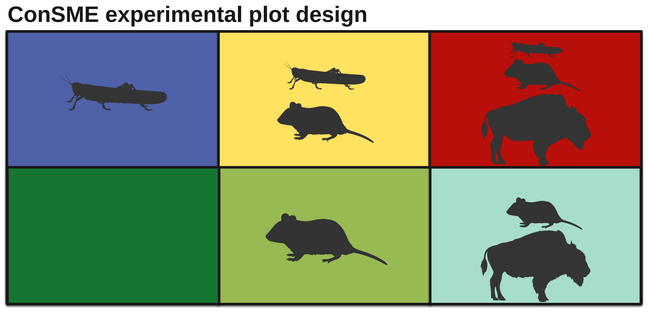


**Fig. 1.** Schematic of one block of the ConSME experimental design. Each color indicates a unique herbivore exclosure treatment. Silhouettes indicate the presence or absence of herbivore guilds (insects, small mammals, bison, or some combination of the three). Colors and silhouettes are consistent with all other figures.

- ConSME: Experimental manipulation of herbivore presence at Konza LTER
  - Manipulation of bison, small mammal, and insect presence, alone and in combination
  - Began in 2019
  - Maintained via fencing & insecticide
  - 18 blocks; 9 in 1-year fire return interval (FRI), 9 in 4-year FRI
- In 2020, exhaustively searched 18 blocks (all herbivore exclosure treatments) for all individuals of *K. eupatorioides*
  - Tagged and mapped individuals
  - Recorded size metrics; correlates strongly with biomass
- In 2021, revisited these block x treatment combinations &
  - Measured biomass & fruit number, scored survival of marked plants
  - Quantified recruitment
  - Calculated population growth rate (λ) for each treatment (across all blocks)
- Quantified herbivore exclosure treatment effects
  - fit a mixed model with herbivore exclosure treatment and initial plant biomass as fixed effects, block as a random effect, with survival, growth, and fruits as the response variables
  - compared all possible subsets of this mixed model to ask whether herbivore exclosure treatment was present in the best-fit model

## Discussion

- Each herbivore guild impacts different vital rates, and has disparate effects on λ
- Some herbivore guilds increase λ and vital rates, others reduce them
- Effects of multiple herbivore guilds together are consistently weaker than each herbivore guild's effect alone
  - This effect could be mediated by abiotic limits to maximum performance: implications for climate change
- Additional mechanisms might also be at play:
  - Safe site availability
  - One herbivore guild changes population response to another guild[4]
  - Changes in herbivore density
- Context-dependence is very common & should be considered when predicting herbivore effects

**Acknowledgements**
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**Literature Cited**

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